

# Sound Texture Perception via Statistics of the Auditory Periphery: Evidence from Sound Synthesis

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## SUMMARY

Rainstorms, insect swarms, and galloping horses produce “sound textures”—the collective result of many similar acoustic events. Sound textures are distinguished by temporal homogeneity, suggesting they could be recognized with time-averaged statistics. To test this hypothesis, we processed real-world textures with an auditory model containing filters tuned for sound frequencies and their modulations, and measured statistics of the resulting decomposition. We then assessed the realism and recognizability of novel sounds synthesized to have matching statistics. Statistics of individual frequency channels, capturing spectral power and sparsity, generally failed to produce compelling synthetic textures; however, combining them with correlations between channels produced identifiable and natural-sounding textures. Synthesis quality declined if statistics were computed from biologically implausible auditory models. The results suggest that sound texture perception is mediated by relatively simple statistics of early auditory representations, presumably computed by downstream neural populations. The synthesis methodology offers a powerful tool for their further investigation.

## INTRODUCTION

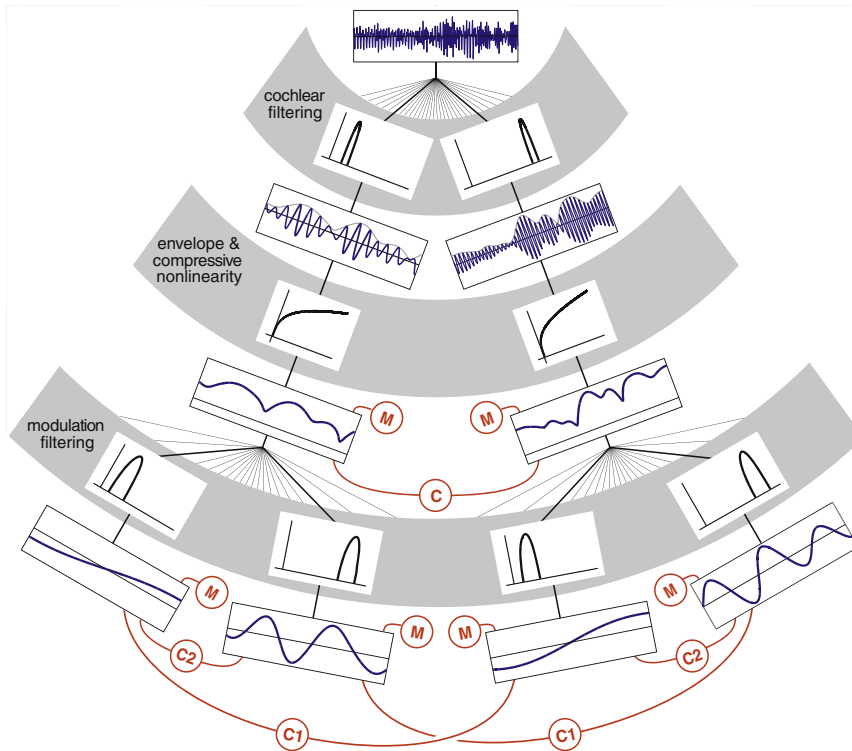
Sensory receptors measure light, sound, skin pressure, and other forms of energy, from which organisms must recognize the events that occur in the world. Recognition is believed to occur via the transformation of sensory input into representations in which stimulus identity is explicit (for instance, via neurons responsive to one category but not others). In the auditory system, as in other modalities, much is known about how this process begins, from transduction through the initial stages of neural processing. Something is also known about the system’s output, reflected in the ability of human listeners to recognize sounds. Less is known about what happens in the middle—the stages between peripheral processing and perceptual decisions. The difficulty of studying these mid-level process-

ing stages partly reflects a lack of appropriate stimuli, as the tones and noises that are staples of classical hearing research do not capture the richness of natural sounds.

Here we study “sound texture,” a category of sound that is well-suited for exploration of mid-level auditory perception. Sound textures are produced by a superposition of many similar acoustic events, such as arise from rain, fire, or a swamp full of insects, and are analogous to the visual textures that have been studied for decades (Julesz, 1962). Textures are a rich and varied set of sounds, and we show here that listeners can readily recognize them. However, unlike the sound of an individual event, such as a footstep, or of the complex temporal sequences of speech or music, a texture is defined by properties that remain constant over time. Textures thus possess a simplicity relative to other natural sounds that makes them a useful starting point for studying auditory representation and sound recognition.

We explored sound texture perception using a model of biological texture representation. The model begins with known processing stages from the auditory periphery and culminates with the measurement of simple statistics of these stages. We hypothesize that such statistics are measured by subsequent stages of neural processing, where they are used to distinguish and recognize textures. We tested the model by conducting psychophysical experiments with synthetic sounds engineered to match the statistics of real-world textures. The logic of the approach, borrowed from vision research, is that if texture perception is based on a set of statistics, two textures with the same values of those statistics should sound the same (Julesz, 1962; Portilla and Simoncelli, 2000). In particular, our synthetic textures should sound like another example of the corresponding real-world texture if the statistics used for synthesis are similar to those measured by the auditory system.

Although the statistics we investigated are relatively simple and were not hand-tuned to specific natural sounds, they produced compelling synthetic examples of many real-world textures. Listeners recognized the synthetic sounds nearly as well as their real-world counterparts. In contrast, sounds synthesized using representations distinct from those in biological auditory systems generally did not sound as compelling. Our results suggest that the recognition of sound textures is based on statistics of modest complexity computed from the responses of the peripheral auditory system. These statistics likely reflect sensitivities of downstream neural populations. Sound textures and their synthesis thus provide a substrate for studying mid-level audition.



**Figure 1. Model Architecture**

A sound waveform (top row) is filtered by a “cochlear” filterbank (gray stripe contains two example filters at different frequencies, on a log-frequency axis). Cochlear filter responses (i.e., subbands) are bandlimited versions of the original signal (third row), the envelopes of which (in gray) are passed through a compressive nonlinearity (gray stripe, fourth row), yielding compressed envelopes (fifth row), from which marginal statistics and cross band correlations are measured. Envelopes are filtered with a modulation filter bank (gray stripe, sixth row, containing two example filters for each of the two example cochlear channels, on a log-frequency axis), the responses of which (seventh row) are used to compute modulation marginals and correlations. Red icons denote statistical measurements: marginal moments of a single signal or correlations between two signals.

## RESULTS

Our investigations of sound texture were constrained by three sources of information: auditory physiology, natural sound statistics, and perceptual experiments. We used the known structure of the early auditory system to construct the initial stages of our model and to constrain the choices of statistics. We then established the plausibility of different types of statistics by verifying that they vary across natural sounds and could thus be useful for their recognition. Finally, we tested the perceptual importance of different texture statistics with experiments using synthetic sounds.

### Texture Model

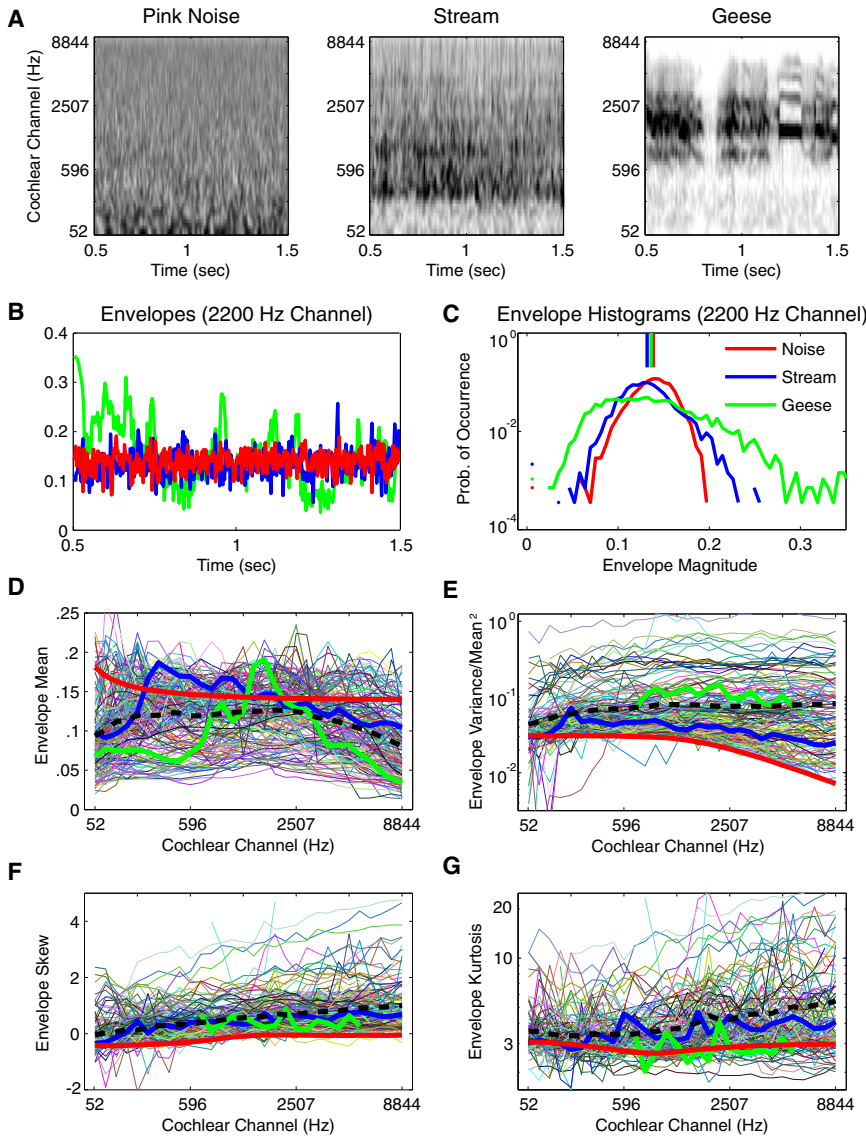
Our model is based on a cascade of two filter banks (Figure 1) designed to replicate the tuning properties of neurons in early stages of the auditory system, from the cochlea through the thalamus. An incoming sound is first processed with a bank of 30 bandpass cochlear filters that decompose the sound waveform into acoustic frequency bands, mimicking the frequency selectivity of the cochlea. All subsequent processing is performed on the amplitude envelopes of these frequency bands. Amplitude envelopes can be extracted from cochlear responses with a low-pass filter and are believed to underlie many aspects of peripheral auditory responses (Joris et al., 2004). When the envelopes are plotted in grayscale and arranged vertically, they form a spectrogram, a two-dimensional (time versus frequency) image commonly used for visual depiction of sound (e.g., Figure 2A). Perceptually, envelopes carry much of the important information in natural sounds (Gygi et al., 2004; Shannon et al., 1995; Smith

et al., 2002), and can be used to reconstruct signals that are perceptually indistinguishable from the original in which the envelopes were measured. Cochlear transduction of sound is also distinguished by amplitude compression (Ruggero, 1992)—the response to high intensity sounds is proportionally smaller than

that to low intensity sounds, due to nonlinear, level-dependent amplification. To simulate this phenomenon, we apply a compressive nonlinearity to the envelopes.

Each compressed envelope is further decomposed using a bank of 20 bandpass modulation filters. Modulation filters are conceptually similar to cochlear filters, except that they operate on (compressed) envelopes rather than the sound pressure waveform, and are tuned to frequencies an order of magnitude lower, as envelopes fluctuate at relatively slow rates. A modulation filter bank is consistent with previous auditory models (Bacon and Grantham, 1989; Dau et al., 1997) as well as reports of modulation tuning in midbrain and thalamic neurons (Baumann et al., 2011; Joris et al., 2004; Miller et al., 2002; Rodríguez et al., 2010). Both the cochlear and modulation filters in our model had bandwidths that increased with their center frequency (such that they were approximately constant on a logarithmic scale), as is observed in biological auditory systems.

From cochlear envelopes and their modulation bands, we derive a representation of texture by computing statistics (red symbols in Figure 1). The statistics are time-averages of nonlinear functions of either the envelopes or the modulation bands. Such statistics are in principle suited to summarizing stationary signals like textures, whose properties are constant over some moderate timescale. A priori, however, it is not obvious whether simple, biologically plausible statistics would have much explanatory power as descriptors of natural sounds or of their perception. Previous attempts to model sound texture have come from the machine audio and sound rendering communities (Athineos and Ellis, 2003; Dubnov et al., 2002; Saint-Arnaud and Popat, 1995; Verron et al., 2009; Zhu and Wyse, 2004) and



**Figure 2. Cochlear Marginal Statistics**

(A) Spectrograms of three sound excerpts, generated by plotting the envelopes of a cochlear filter decomposition. Gray-level indicates the (compressed) envelope amplitude (same scale for all three sounds). (B) Envelopes of one cochlear channel for the three sounds from (A). (C) Histograms (gathered over time) of the envelopes in (B). Vertical line segments indicate the mean value of the envelope for each sound. (D–G) Envelope marginal moments for each cochlear channel of each of 168 natural sound textures. Moments of sounds in (A–C) are plotted with thick lines; dashed black line plots the mean value of each moment across all sounds.

resentation of visual texture (Heeger and Bergen, 1995; Portilla and Simoncelli, 2000), which provided inspiration for our work. Both types of statistic were computed on cochlear envelopes as well as their modulation bands (Figure 1). Because modulation filters are applied to the output of a particular cochlear channel, they are tuned in both acoustic frequency and modulation frequency. We thus distinguished two types of modulation correlations: those between bands tuned to the same modulation frequency but different acoustic frequencies (C1), and those between bands tuned to the same acoustic frequency but different modulation frequencies (C2).

To provide some intuition for the variation in statistics that occurs across sounds, consider the cochlear marginal moments: statistics that describe the distribution of the envelope amplitude for a single cochlear channel. Figure 2A shows the envelopes, displayed as spectrograms, for excerpts of three example

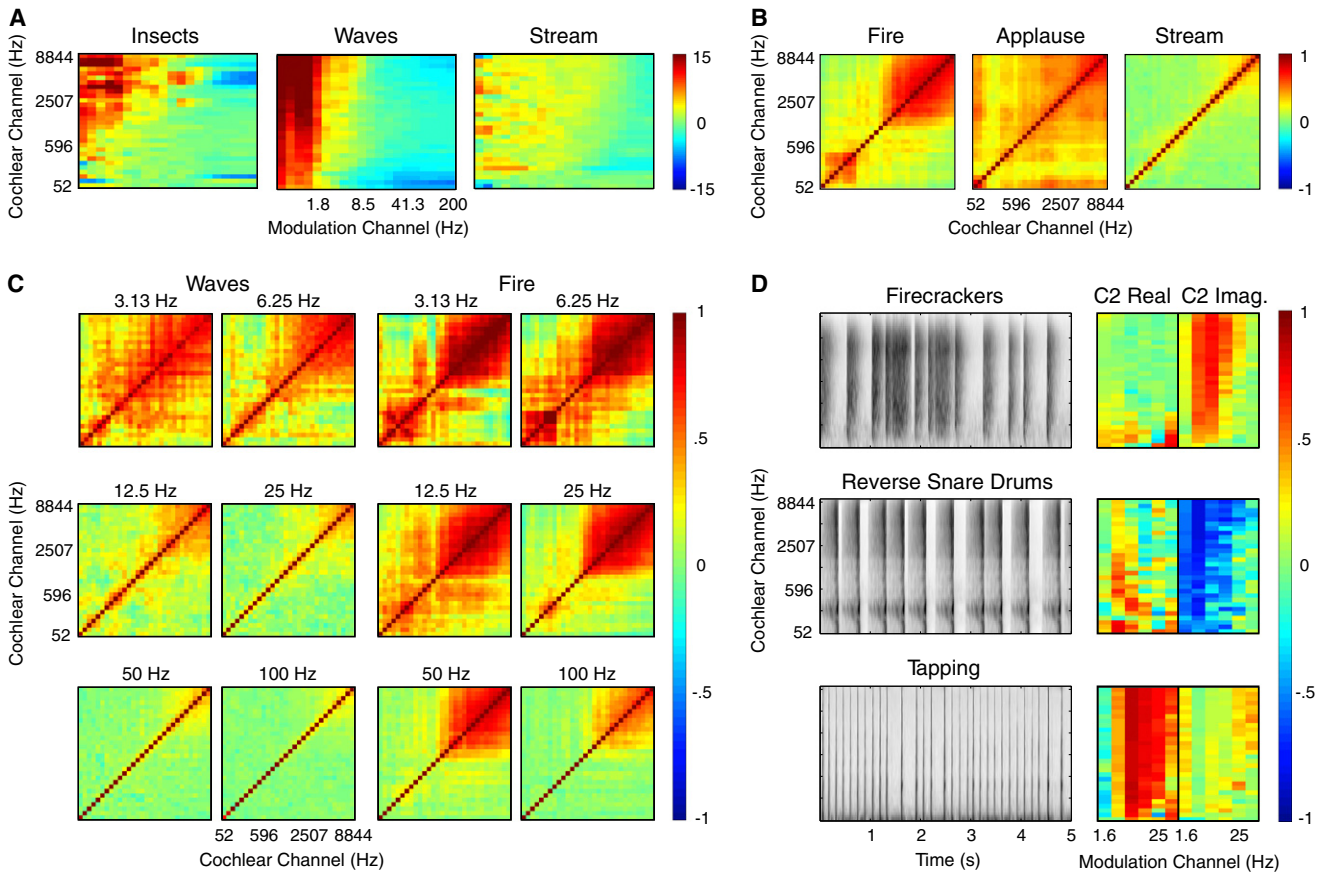
sounds (pink [1/f] noise, a stream, and geese calls), and Figure 2B plots the envelopes of one particular channel for each sound. It is visually apparent that the envelopes of the three sounds are distributed differently—those of the geese contain more high-amplitude and low-amplitude values than those of the stream or noise. Figure 2C shows the envelope distributions for one cochlear channel. Although the mean envelope values are nearly equal in this example (because they have roughly the same average acoustic power in that channel), the envelope distributions differ in width, asymmetry about the mean, and the presence of a long positive tail. These properties can be captured by the marginal moments (mean, variance, skew, and kurtosis, respectively). Figures 2D–2G show these moments for our full set of sound textures. Marginal moments have previously been proposed to play a role in envelope discrimination (Lorenzi et al., 1999; Strickland and Viemeister, 1996), and often reflect

**Texture Statistics**

have involved representations unrelated to those in biological auditory systems. Of all the statistics the brain could compute, which might be used by the auditory system? Natural sounds can provide clues: in order for a statistic to be useful for recognition, it must produce different values for different sounds. We considered a set of generic statistics and verified that they varied substantially across a set of 168 natural sound textures.

We examined two general classes of statistic: marginal moments and pairwise correlations. Both types of statistic involve averages of simple nonlinear operations (e.g., squaring, products) that could plausibly be measured using neural circuitry at a later stage of neural processing. Moments and correlations derive additional plausibility from their importance in the repre-

sentation of visual texture (Heeger and Bergen, 1995; Portilla and Simoncelli, 2000), which provided inspiration for our work. Both types of statistic were computed on cochlear envelopes as well as their modulation bands (Figure 1). Because modulation filters are applied to the output of a particular cochlear channel, they are tuned in both acoustic frequency and modulation frequency. We thus distinguished two types of modulation correlations: those between bands tuned to the same modulation frequency but different acoustic frequencies (C1), and those between bands tuned to the same acoustic frequency but different modulation frequencies (C2).



**Figure 3. Modulation Power and Correlation Statistics**

(A) Modulation power in each band (normalized by the variance of the corresponding cochlear envelope) for insects, waves, and stream sounds of Figure 4B. For ease of display and interpretation, this statistic is expressed in dB relative to the same statistic for pink noise.

(B) Cross-band envelope correlations for fire, applause, and stream sounds of Figure 4B. Each matrix cell displays the correlation coefficient between a pair of cochlear envelopes.

(C) C1 correlations for waves and fire sounds of Figure 4B. Each matrix contains correlations between modulation bands tuned to the same modulation frequency but to different acoustic frequencies, yielding matrices of the same format as (B), but with a different matrix for each modulation frequency, indicated at the top of each matrix.

(D) Spectrograms and C2 correlations for three sounds. Note asymmetric envelope shapes in first and second rows, and that abrupt onsets (top), offsets (middle), and impulses (bottom) produce distinct correlation patterns. In right panels, modulation channel labels indicate the center of low-frequency band contributing to the correlation. See also Figure S6.

the property of sparsity, which tends to characterize natural sounds and images (Field, 1987; Attias and Schreiner, 1998). Intuitively, sparsity reflects the discrete events that generate natural signals; these events are infrequent, but produce a burst of energy when they occur, yielding high-variance amplitude distributions. Sparsity has been linked to sensory coding (Field, 1987; Olshausen and Field, 1996; Smith and Lewicki, 2006), but its role in the perception of real-world sounds has been unclear.

Each of the remaining statistics we explored (Figure 1) captures distinct aspects of acoustic structure and also exhibits large variation across sounds (Figure 3). The moments of the modulation bands, particularly the variance, indicate the rates at which cochlear envelopes fluctuate, allowing distinction between rapidly modulated sounds (e.g., insect vocalizations) and slowly modulated sounds (e.g., ocean waves). The correlation statistics, in contrast, each reflect distinct aspects of cor-

relation between envelopes of different channels, or between their modulation bands. The cochlear correlations (C) distinguish textures with broadband events that activate many channels simultaneously (e.g., applause), from those that produce nearly independent channel responses (many water sounds; see Experiment 1: Texture Identification). The cross-channel modulation correlations (C1) are conceptually similar except that they are computed on a particular modulation band of each cochlear channel. In some sounds (e.g., wind, or waves) the C1 correlations are large only for low modulation-frequency bands, whereas in others (e.g., fire) they are present across all bands. The within-channel modulation correlations (C2) allow discrimination between sounds with sharp onsets or offsets (or both), by capturing the relative phase relationships between modulation bands within a cochlear channel. See Experimental Procedures for detailed descriptions.

### Sound Synthesis

Our goal in synthesizing sounds was not to render maximally realistic sounds per se, as in most sound synthesis applications (Dubnov et al., 2002; Verron et al., 2009), but rather to test hypotheses about how the brain represents sound texture, using realism as an indication of the hypothesis validity. Others have also noted the utility of synthesis for exploring biological auditory representations (Mesgarani et al., 2009; Slaney, 1995); our work is distinct for its use of statistical representations. Inspired by methods for visual texture synthesis (Heeger and Bergen, 1995; Portilla and Simoncelli, 2000), our method produced novel signals that matched some of the statistics of a real-world sound. If the statistics used to synthesize the sound are similar to those used by the brain for texture recognition, the synthetic signal should sound like another example of the original sound.

To synthesize a texture, we first obtained desired values of the statistics by measuring the model responses (Figure 1) for a real-world sound. We then used an iterative procedure to modify a random noise signal (using variants of gradient descent) to force it to have these desired statistic values (Figure 4A). By starting from noise, we hoped to generate a signal that was as random as possible, constrained only by the desired statistics.

Figure 4B displays spectrograms of several naturally occurring sound textures along with synthetic examples generated from their statistics (see Figure S1 available online for additional examples). It is visually apparent that the synthetic sounds share many structural properties of the originals, but also that the process has not simply regenerated the original sound—here and in every other example we examined, the synthetic signals were physically distinct from the originals (see also Experiment 1: Texture Identification [Experiment 1b, condition 7]). Moreover, running the synthesis procedure multiple times produced exemplars with the same statistics but whose spectrograms were easily discriminated visually (Figure S2). The statistics we studied thus define a large set of sound signals (including the original in which the statistics are measured), from which one member is drawn each time the synthesis process is run.

To assess whether the synthetic results sound like the natural textures whose statistics they matched, we conducted several experiments. The results can also be appreciated by listening to example synthetic sounds, available online ([http://www.cns.nyu.edu/~lcv/sound\\_texture.html](http://www.cns.nyu.edu/~lcv/sound_texture.html)).

### Experiment 1: Texture Identification

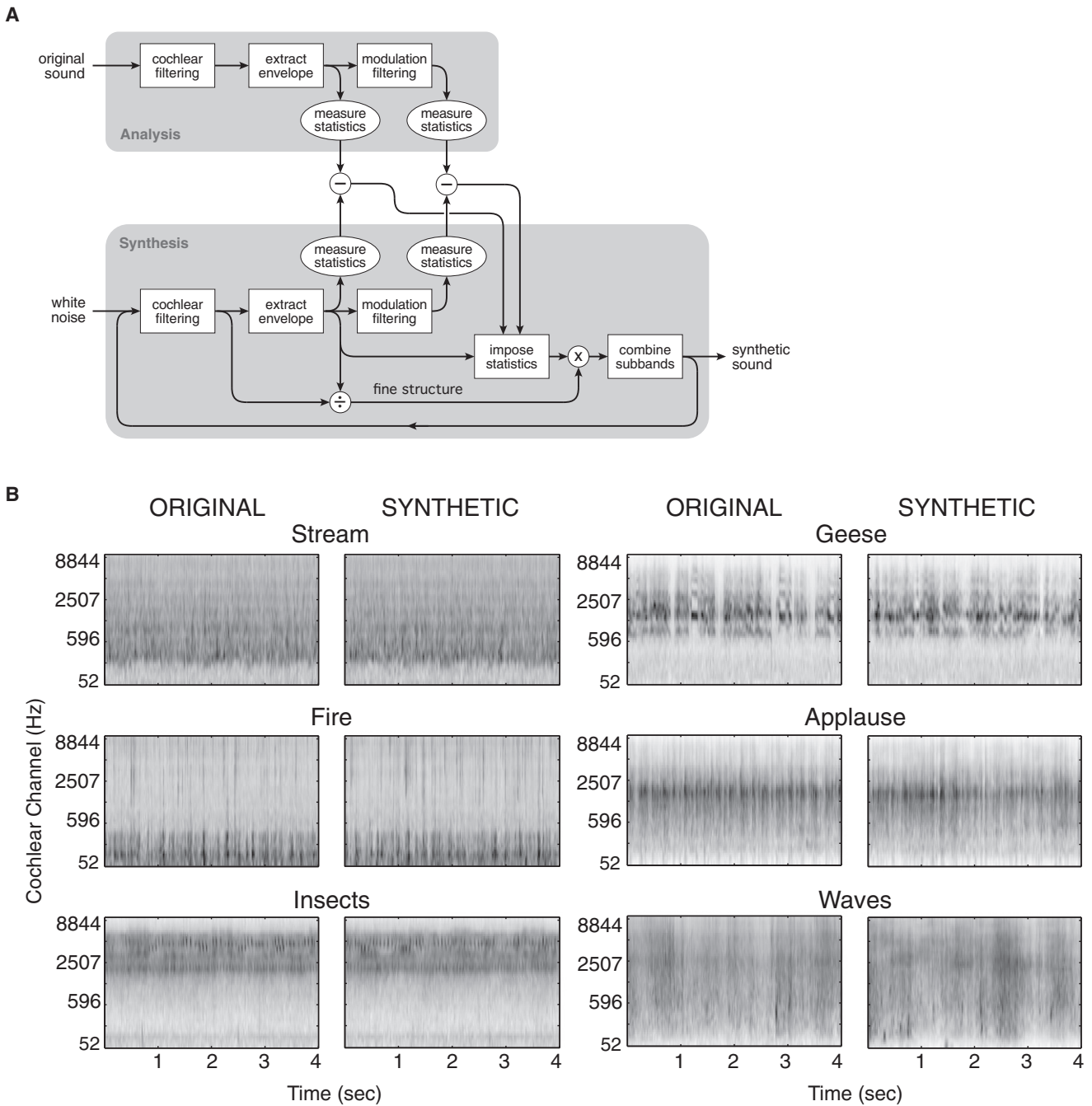
We first tested whether synthetic sounds could be identified as exemplars of the natural sound texture from which their statistics were obtained. Listeners were presented with example sounds, and chose an identifying name from a set of five. In Experiment 1a, sounds were synthesized using different subsets of statistics. Identification was poor when only the cochlear channel power was imposed (producing a sound with roughly the same power spectrum as the original), but improved as additional statistics were included as synthesis constraints (Figure 5A;  $F[2.25, 20.25] = 124.68$ ,  $p < 0.0001$ ; see figure for paired comparisons between conditions). Identifiability of textures synthesized using the full model approached that obtained for the original sound recordings.

Inspection of listeners' responses revealed several results of interest (Figures 5B and 5C). In condition 1, when only the cochlear channel power was imposed, the sounds most often correctly identified were those that are noise-like (wind, static, etc.); such sounds were also the most common incorrect answers. This is as expected, because the synthesis process was initialized with noise and in this condition simply altered its spectrum. A more interesting pattern emerged for condition 2, in which the cochlear marginal moments were imposed. In this condition, but not others, the sounds most often identified correctly, and chosen incorrectly, were water sounds. This is readily apparent from listening to the synthetic examples—water often sounds realistic when synthesized from its cochlear marginals, and most other sounds synthesized this way sound water-like.

Because the cochlear marginal statistics only constrain the distribution of amplitudes within individual frequency channels, this result suggests that the salient properties of water sounds are conveyed by sparsely distributed, independent, bandpass acoustic events. In Experiment 1b, we further explored this result: in conditions 1 and 2 we again imposed marginal statistics, but used filters that were either narrower or broader than the filters found in biological auditory systems. Synthesis with these alternative filters produced overall levels of performance similar to the auditory filter bank (condition 3; Figure 5D), but in both cases, water sounds were no longer the most popular choices (Figures 5E and 5F; the four water categories were all identified less well, and chosen incorrectly less often, in conditions 1 and 2 compared to condition 3;  $p < 0.01$ , sign test). It thus seems that the bandwidths of biological auditory filters are comparable to those of the acoustic events produced by water (see also Figure S3), and that water sounds often have remarkably simple structure in peripheral auditory representations.

Although cochlear marginal statistics are adequate to convey the sound of water, in general they are insufficient for recognition (Figure 5A). One might expect that with a large enough set of filters, marginal statistics alone would produce better synthesis, because each filter provides an additional set of constraints on the sound signal. However, our experiments indicate otherwise. When we synthesized sounds using a filter bank with the bandwidths of our canonical model, but with four times as many filters (such that adjacent filters overlapped more than in the original filter bank), identification was not significantly improved [Figure 5D; condition 4 versus 3,  $t(9) = 1.27$ ,  $p = 0.24$ ]. Similarly, one might suppose that constraining the full marginal distribution (as opposed to just matching the four moments in our model) might capture more structure, but we found that this also failed to produce improvements in identification [Figure 5D; condition 5 versus 3,  $t(9) = 1.84$ ,  $p = 0.1$ ; Figure S4]. These results suggest that cochlear marginal statistics alone, irrespective of how exhaustively they are measured, cannot account for our perception of texture.

Because the texture model is independent of the signal length, we could measure statistics from signals much shorter or longer than those being synthesized. In both cases the results generally sounded as compelling as if the synthetic and original signals were the same length. To verify this empirically, in condition 7



**Figure 4. Synthesis Algorithm and Example Results**

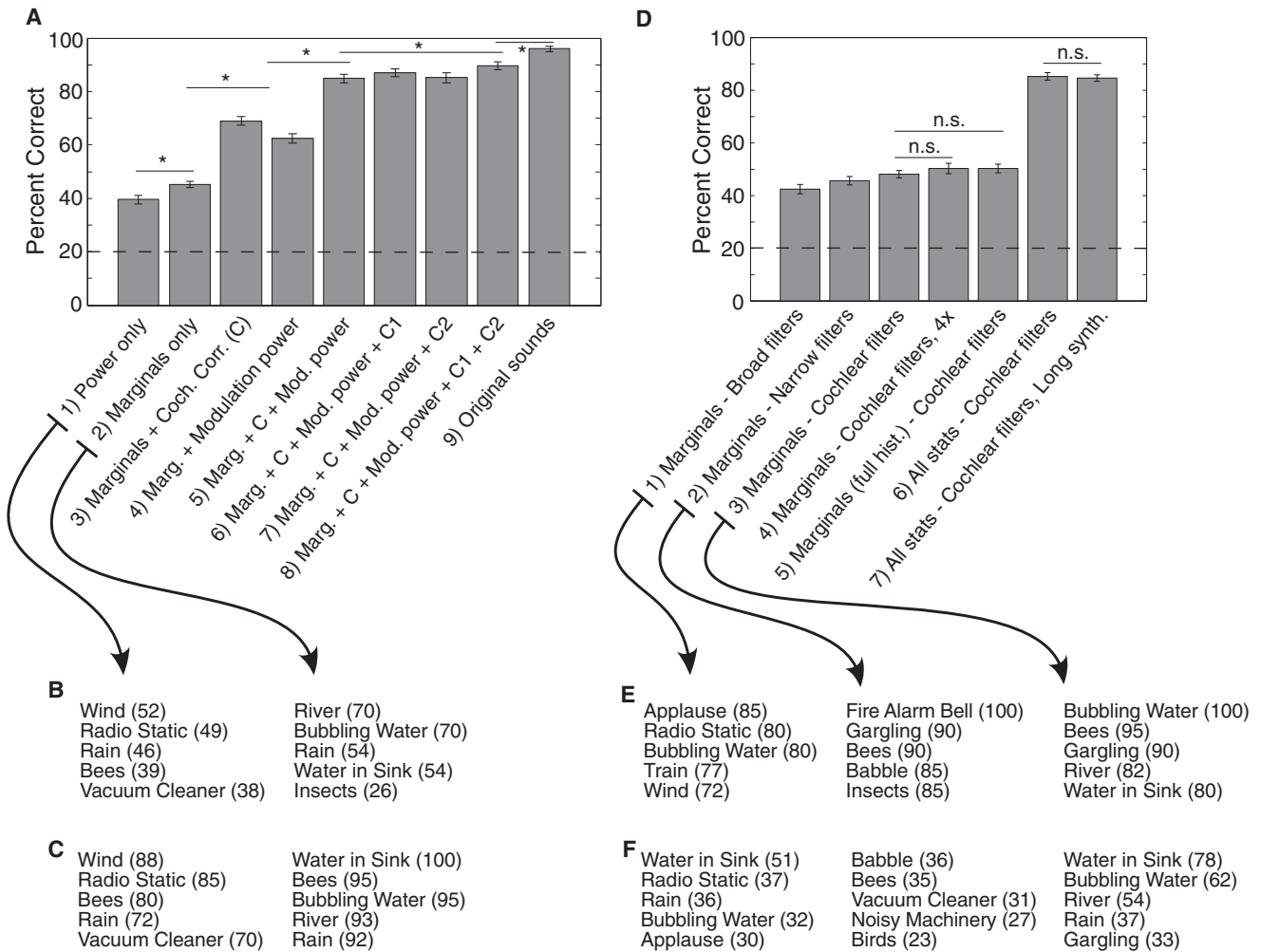
(A) Schematic of synthesis procedure. Statistics are measured after a sound recording is passed through the auditory model of Figure 1. Synthetic signal is initialized as noise, and the original sound's statistics are imposed on its cochlear envelopes. The modified envelopes are multiplied by their associated fine structure, and then recombined into a sound signal. The procedure is iterated until the synthesized signal has the desired statistics.

(B) Spectrograms of original and synthetic versions of several sounds (same amplitude scale for all sounds). See also Figure S1 and Figure S2.

we used excerpts of 15 s signals synthesized from 7 s originals. Identification performance was unaffected [Figure 5D; condition 7 versus 6;  $t(9) = 0.5$ ,  $p = 0.63$ ], indicating that these longer signals captured the texture qualities as well as signals more comparable to the original signals in length.

**Experiment 2: Necessity of Each Class of Statistic**

We found that each class of statistic was perceptually necessary, in that its omission from the model audibly impaired the quality of some synthetic sounds. To demonstrate this empirically, in Experiment 2a we presented listeners with excerpts



**Figure 5. Experiment 1: Texture Identification**

(A) Identification improves as more statistics are included in the synthesis. Asterisks denote significant differences between conditions,  $p < 0.01$  (paired t tests, corrected for multiple comparisons). Here and elsewhere, error bars denote standard errors and dashed lines denote the chance level of performance.

(B) The five categories correctly identified most often for conditions 1 and 2, with mean percent correct in parentheses.

(C) The five categories chosen incorrectly most often for conditions 1 and 2, with mean percent trials chosen (of those where they were a choice) in parentheses.

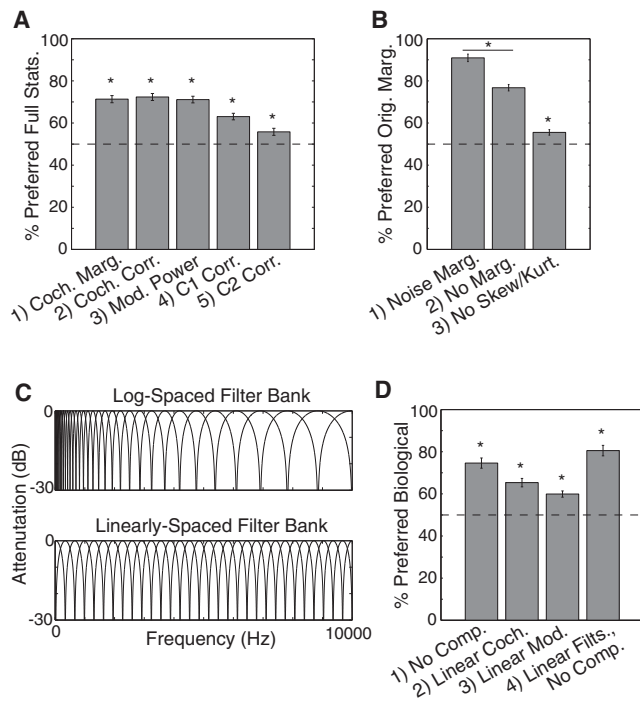
(D) Identification with alternative marginal statistics, and long synthetic signals. Horizontal lines indicate nonsignificant differences ( $p > 0.05$ ).

(E and F) The five (E) most correctly identified and (F) most often incorrectly chosen categories for conditions 1–3. See also Figure S3 and Figure S4.

of original texture recordings followed by two synthetic versions—one synthesized using the full set of model statistics, and the other synthesized with one class omitted—and asked them to judge which synthetic version sounded more like the original. Figure 6A plots the percentage of trials on which the full set of statistics was preferred. In every condition, this percentage was greater than that expected by chance (t tests,  $p < 0.01$  in all cases, Bonferroni corrected), though the preference was stronger for some statistic classes than others [ $F(4,36) = 15.39$ ,  $p < 0.0001$ ].

The effect of omitting a statistic class was not noticeable for every texture. A potential explanation is that the statistics of many textures are close to those of noise for some subset of statistics, such that omitting that subset does not cause the statistics of the synthetic result to deviate much from the correct

values (because the synthesis is initialized with noise). To test this idea, we computed the difference between each sound's statistics and those of pink ( $1/f$ ) noise, for each of the five statistic classes. When we reanalyzed the data including only the 30% of sounds whose statistics were most different from those of noise, the proportion of trials on which the full set of statistics was preferred was significantly higher in each case (t tests,  $p < 0.05$ ). Including a particular statistic in the synthesis process thus tends to improve realism when the value of that statistic deviates from that of noise. Because of this, not all statistics are necessary for the synthesis of every texture (although all statistics presumably contribute to the perception of every texture—if the values were actively perturbed from their correct values, whether noise-like or not, we found that listeners generally noticed).



**Figure 6. Experiments 2 and 3: Omitting and Manipulating Statistics**

(A) Experiment 2a: synthesis with the full set of statistics is preferred over synthesis omitting any single class. Condition labels indicate statistic class omitted. In condition 1, the envelope mean was imposed, to ensure that the spectrum was approximately correct. Asterisks denote significant differences from chance,  $p < 0.01$ .

(B) Experiment 2b: sounds with the correct cochlear marginal statistics were preferred over those with (1), the cochlear marginal moments of noise; (2), all cochlear marginals omitted (as in condition 1 of [A]); or (3), the skew and kurtosis omitted. Asterisks denote significant differences from chance or between conditions,  $p < 0.01$ .

(C) Frequency responses of logarithmically and linearly spaced cochlear filter banks.

(D) Experiment 3: sounds synthesized with a biologically plausible auditory model were preferred over those synthesized with models deviating from biology (by omitting compression, or by using linearly spaced cochlear or modulation filter banks). Asterisks denote significant differences from chance,  $p < 0.01$ .

We expected that the C2 correlation, which measures phase relations between modulation bands, would help capture the temporal asymmetry of abrupt onsets or offsets. To test this idea, we separately analyzed sounds that visually or audibly possessed such asymmetries (explosions, drum beats, etc.). For this subset of sounds, and for other randomly selected subsets, we computed the average proportion of trials in which synthesis with the full set of statistics was preferred over that with the C2 correlation omitted. The preference for the full set of statistics was larger in the asymmetric sounds than in 99.96% of other subsets, confirming that the C2 correlations were particularly important for capturing asymmetric structure.

It is also notable that omitting the cochlear marginal moments produced a noticeable degradation in realism for a large fraction of sounds, indicating that the sparsity captured by these statistics is perceptually important. As a further test, we explicitly

forced sounds to be nonsparse and examined the effect on perception. We synthesized sounds using a hybrid set of statistics in which the envelope variance, skew, and kurtosis were taken from pink noise, with all other statistics given the correct values for a particular real-world sound. Because noise is nonsparse (the marginals of noise lie at the lower extreme of the values for natural sounds; Figure 2), this manipulation forced the resulting sounds to lack sparsity but to maintain the other statistical properties of the original sound. We found that the preference for signals with the correct marginals was enhanced in this condition [1 versus 2,  $t(9) = 8.1$ ,  $p < 0.0001$ ; Figure 6B], consistent with the idea that sparsity is perceptually important for most natural sound textures. This result is also an indication that the different classes of statistic are not completely independent: constraining the other statistics had some effect on the cochlear marginals, bringing them closer to the values of the original sound even if they themselves were not explicitly constrained. We also found that listeners preferred sounds synthesized with all four marginal moments to those with the skew and kurtosis omitted ( $t(8) = 4.1$ ,  $p = 0.003$ ). Although the variance alone contributes substantially to sparsity, the higher-order moments also play some role.

### Experiment 3: Statistics of Nonbiological Sound Representations

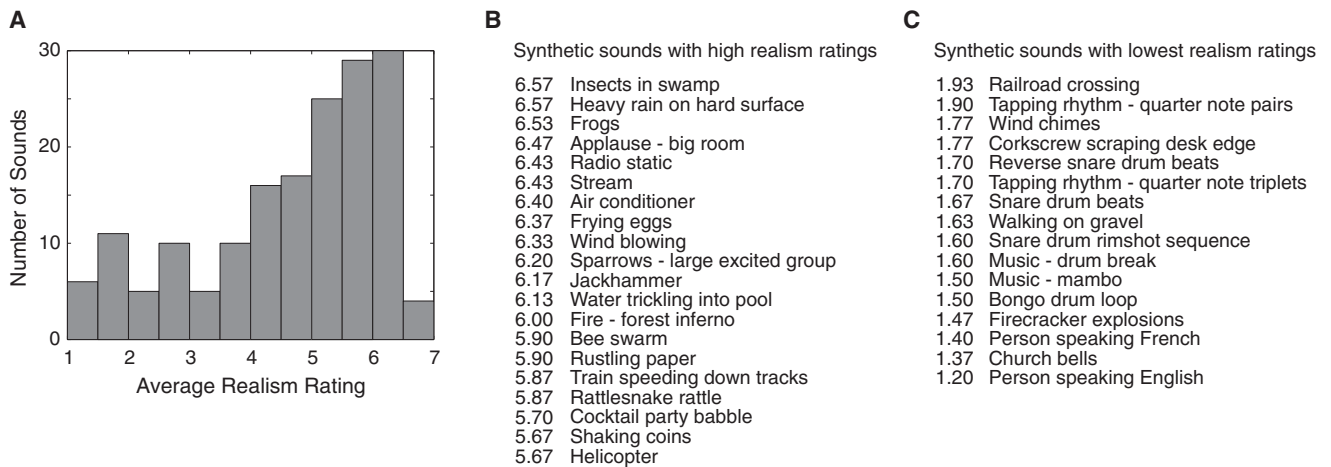
How important are the biologically inspired features of our model? One might expect that any large and varied set of statistics would produce signals that resemble the originals. As a test, we altered our model in three respects: (1) removing cochlear compression, (2), altering the bandwidths of the “cochlear” filters, and (3) altering the bandwidths of the modulation filters (rows four, two, and six of Figure 1). In the latter two cases, linearly spaced filter banks were substituted for the log-spaced filter banks found in biological auditory systems (Figure 6C). We also included a condition with all three alterations. Each altered model was used both to measure the statistics in the original sound signal, and to impose them on synthetic sounds. In all cases, the number of filters was preserved, and thus all models had the same number of statistics.

We again performed an experiment in which listeners judged which of two synthetic sounds (one generated from our biologically inspired model, the other from one of the nonbiological models) more closely resembled the original from which their statistics were measured. In each condition, listeners preferred synthetic sounds produced by the biologically inspired model (Figure 6D; sign tests,  $p < 0.01$  in all conditions), supporting the notion that the auditory system represents textures using statistics similar to those in this model.

### Experiment 4: Realism Ratings

To illustrate the overall effectiveness of the synthesis, we measured the realism of synthetic versions of every sound in our set. Listeners were presented with an original recording followed by a synthetic signal matching its statistics. They rated the extent to which the synthetic signal was a realistic example of the original sound, on a scale of 1–7. Most sounds yielded average ratings above 4 (Figures 7A and 7B; Table S1). The sounds with low ratings, however, are of particular interest, as they are





**Figure 7. Experiment 4: Realism Ratings**

(A) Histogram of average realism ratings for each sound in our set.

(B) List of 20 sound textures with high average ratings. Multiple examples of similar sounds are omitted for brevity.

(C) List of all sounds with average realism ratings <2, along with their average rating. See Table S1 for complete list. See also Figure S5.

statistically matched to the original recordings and yet do not sound like them. Figure 7C lists the sounds with average ratings below 2. They fall into three general classes—those involving pitch (railroad crossing, wind chimes, music, speech, bells), rhythm (tapping, music, drumming), and reverberation (drum beats, firecrackers); see also Figure S5. This suggests that the perception of these sound attributes involves measurements substantially different from those in our model.

## DISCUSSION

We have studied “sound textures,” a class of sounds produced by multiple superimposed acoustic events, as are common to many natural environments. Sound textures are distinguished by temporal homogeneity, and we propose that they are represented in the auditory system with time-averaged statistics. We embody this hypothesis in a model based on statistics (moments and correlations) of a sound decomposition like that found in the subcortical auditory system. To test the role of these statistics in texture recognition, we conducted experiments with synthetic sounds matching the statistics of various real-world textures. We found that (1) such synthetic sounds could be accurately recognized, and at levels far better than if only the spectrum or sparsity was matched, (2) eliminating subsets of the statistics in the model reduced the realism of the synthetic results, (3) modifying the model to less faithfully mimic the mammalian auditory system also reduced the realism of the synthetic sounds, and (4) the synthetic results were often realistic, but failed markedly for a few particular sound classes.

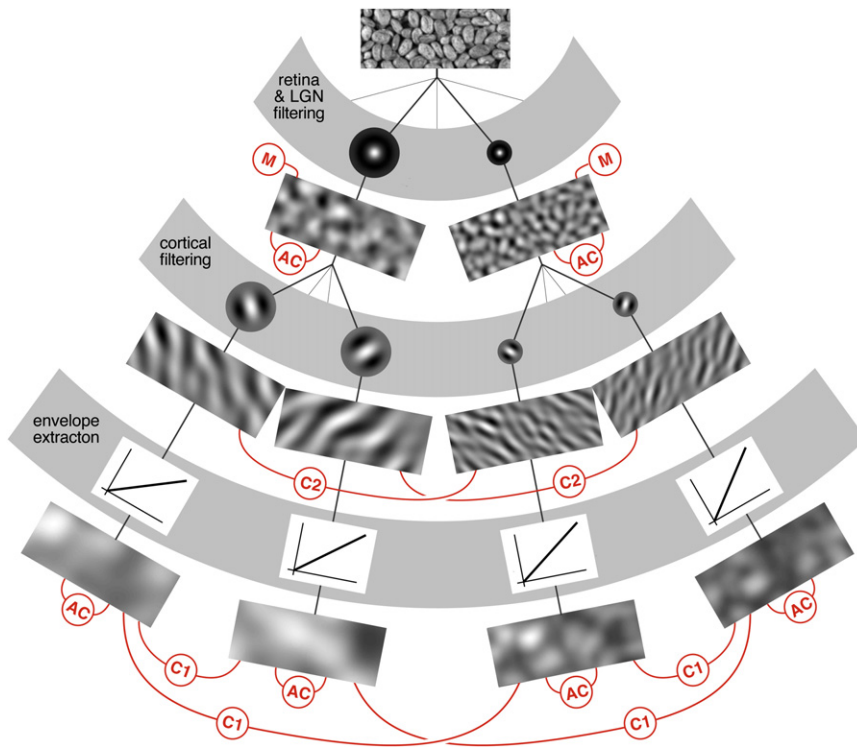
Our results suggest that when listeners recognize the sound of rain, fire, insects, and other such sounds, they are recognizing statistics of modest complexity computed from the output of the peripheral auditory system. These statistics are likely measured at downstream stages of neural processing, and thus provide clues to the nature of mid-level auditory computations.

## Neural Implementation

Because texture statistics are time averages, their computation can be thought of as involving two steps: a nonlinear function applied to the relevant auditory response(s), followed by an average over time. A moment, for instance, could be computed by a neuron that averages its input (e.g., a cochlear envelope) after raising it to a power (two for the variance, three for the skew, etc.). We found that envelope moments were crucial for producing naturalistic synthetic sounds. Envelope moments convey sparsity, a quality long known to differentiate natural signals from noise (Field, 1987) and one that is central to many recent signal-processing algorithms (Asari et al., 2006; Bell and Sejnowski, 1996). Our results thus suggest that sparsity is represented in the auditory system and used to distinguish sounds. Although definitive characterization of the neural locus awaits, neural responses in the midbrain often adapt to particular amplitude distributions (Dean et al., 2005; Kvale and Schreiner, 2004), raising the possibility that envelope moments may be computed subcortically. The modulation power (also a marginal moment) at particular rates also seems to be reflected in the tuning of many thalamic and midbrain neurons (Joris et al., 2004).

The other statistics in our model are correlations. A correlation is the average of a normalized product (e.g., of two cochlear envelopes), and could be computed as such. However, a correlation can also be viewed as the proportion of variance in one variable that is shared by another, which is partly reflected in the variance of the sum of the variables. This formulation provides an alternative implementation (see Experimental Procedures), and illustrates that correlations in one stage of representation (e.g., bandpass cochlear channels) can be reflected in the marginal statistics of the next (e.g., cortical neurons that sum input from multiple channels), assuming appropriate convergence. All of the texture statistics we have considered could thus reduce to marginal statistics at different stages of the auditory system.

Neuronal tuning to texture statistics could be probed using synthetic stimuli whose statistics are parametrically varied.



**Figure 8. Analogous Model of Visual Texture Representation**

Model is depicted in a format like that of the auditory texture model in Figure 1. An image of beans (top row) is filtered into spatial frequency bands by center-surround filters (second row), as happens in the retina/LGN. The spatial frequency bands (third row) are filtered again by orientation selective filters (fourth row) analogous to V1 simple cells, yielding scale and orientation filtered bands (fifth row). The envelopes of these bands are extracted (sixth row) to produce analogs of V1 complex cell responses (seventh row). The linear function at the envelope extraction stage indicates the absence of the compressive nonlinearity present in the auditory model. As in Figure 1, red icons denote statistical measurements: marginal moments of a single signal (M) or correlations between two signals (AC, C1, or C2 for autocorrelation, cross-band correlation, or phase-adjusted correlation). C1 and C2 here and in Figure 1 denote conceptually similar statistics. The autocorrelation (AC) is identical to C1 except that it is computed within a channel. This model is a variant of Portilla and Simoncelli (2000).

Stationary artificial sounds have a long history of use in psychoacoustics and neurophysiology, with recent efforts to incorporate naturalistic statistical structure (Attias and Schreiner, 1998; Garcia-Lazaro et al., 2006; McDermott et al., 2011; Overath et al., 2008; Rieke et al., 1995; Singh and Theunissen, 2003). Stimuli synthesized from our model capture naturally occurring sound structure while being precisely characterized within an auditory model. They offer a middle ground between natural sounds and the tones and noises of classical hearing research.

### Relation to Visual Texture

Visual textures, unlike their auditory counterparts, have been studied intensively for decades (Julesz, 1962), and our work was inspired by efforts to understand visual texture using synthesis (Heeger and Bergen, 1995; Portilla and Simoncelli, 2000; Zhu et al., 1997). How similar are visual and auditory texture representations? For ease of comparison, Figure 8 shows a model diagram of the most closely related visual texture model (Portilla and Simoncelli, 2000), analogous in format to our auditory model (Figure 1) but with input signals and representational stages that vary spatially rather than temporally. The vision model has two stages of linear filtering (corresponding to LGN cells and V1 simple cells) followed by envelope extraction (corresponding to V1 complex cells), whereas the auditory model has the envelope operation sandwiched between linear filtering operations (corresponding to the cochlea and midbrain/thalamus), reflecting structural differences in the two systems. There are also notable differences in the stages at which statistics are computed in the two models: several types of visual texture statistics are computed directly on the initial linear filtering stages, whereas the auditory statistics all follow the envelope

operation, reflecting the primary locus of structure in images versus sounds. However, the statistical computations

themselves—marginal moments and correlations—are conceptually similar in the two models. In both systems, relatively simple statistics capture texture structure, suggesting that texture perception, like filling in (McDermott and Oxenham, 2008; Warren et al., 1972), and saliency (Cusack and Carlyon, 2003; Kayser et al., 2005), may involve analogous computations across modalities.

It will be interesting to explore whether the similarities between modalities extend to inattention, to which visual texture is believed to be robust (Julesz, 1962). Under conditions of focused listening, we are often aware of individual events composing a sound texture, presumably in addition to registering time-averaged statistics that characterize the texture qualities. A classic example is the “cocktail party problem,” in which we attend to a single person talking in a room dense with conversations (Bee and Micheyl, 2008; McDermott, 2009). Without attention, individual voices or other sound sources are likely inaccessible, but we may retain access to texture statistics that characterize the combined effect of multiple sources, as is apparently the case in vision (Alvarez and Oliva, 2009). This possibility could be tested in divided attention experiments with synthetic textures.

### Texture Extensions

We explored the biological representation of sound texture using a set of generic statistics and a relatively simple auditory model, both of which could be augmented in interesting ways. The three sources of information that contributed to the present work—auditory neuroscience, natural sound analysis, and perceptual experiments—all provide directions for such extensions.

The auditory model of Figure 1, from which statistics are computed, captures neuronal tuning characteristics of subcortical

structures. Incorporating cortical tuning properties would likely extend the range of textures we can account for. For instance, cortical receptive fields have spectral tuning that is more complex and varied than that found subcortically (Barbour and Wang, 2003; Depireux et al., 2001), and statistics of filters modeled on their properties could capture higher-order structure that our current model does not. As discussed earlier, the correlations computed on subcortical representations could then potentially be replaced by marginal statistics of filters at a later stage.

It may also be possible to derive additional or alternative texture statistics from an analysis of natural sounds, similar in spirit to previous derivations of cochlear and V1 filters from natural sounds and images (Olshausen and Field, 1996; Smith and Lewicki, 2006), and consistent with other examples of congruence between properties of perceptual systems and natural environments (Attias and Schreiner, 1998; Garcia-Lazaro et al., 2006; Lesica and Grothe, 2008; Nelken et al., 1999; Rieke et al., 1995; Rodríguez et al., 2010; Schwartz and Simoncelli, 2001; Woolley et al., 2005). We envision searching for statistics that vary maximally across sounds and would thus be optimal for recognition.

The sound classes for which the model failed to produce convincing synthetic examples (revealed by Experiment 4) also provide directions for exploration. Notable failures include textures involving pitched sounds, reverberation, and rhythmic structure (Figure 7, Table S1, and Figure S5). It was not obvious a priori that these sounds would produce synthesis failures—they each contain spectral and temporal structures that are stationary (given a moderately long time window), and we anticipated that they might be adequately constrained by the model statistics. However, our results show that this is not the case, suggesting that the brain is measuring something that the model is not.

Rhythmic structure might be captured with another stage of envelope extraction and filtering, applied to the modulation bands. Such filters would measure “second-order” modulation of modulation (Lorenzi et al., 2001), as is common in rhythmic sounds. Alternatively, rhythm could involve a measure specifically of periodic modulation patterns. Pitch and reverberation may also implicate dedicated mechanisms. Pitch is largely conveyed by harmonically related frequencies, which are not made explicit by the pair-wise correlations across frequency found in our current model (see also Figure S5). Accounting for pitch is thus likely to require a measure of local harmonic structure (de Cheveigne, 2004). Reverberation is also well understood from a physical generative standpoint, as linear filtering of a sound source by the environment (Gardner, 1998), and is used to judge source distance (Zahorik, 2002) and environment properties. However, a listener has access only to the result of environmental filtering, not to the source or the filter, implying that reverberation must be reflected in something measured from the sound signal (i.e., a statistic). Our synthesis method provides an unexplored avenue for testing theories of the perception of these sound properties.

One other class of failures involved mixtures of two sounds that overlap in peripheral channels but are acoustically distinct, such as broadband clicks and slow bandpass modulations.

These failures likely result because the model statistics are averages over time, and combine measurements that should be segregated. This suggests a more sophisticated form of estimating statistics, in which averaging is performed after (or in alternation with) some sort of clustering operation, a key ingredient in recent models of stream segregation (Elhilali and Shamma, 2008).

### Using Texture to Understand Recognition

Recognition is challenging because the sensory input arising from different exemplars of a particular category in the world often varies substantially. Perceptual systems must process their input to obtain representations that are invariant to the variation within categories, while maintaining selectivity between categories (DiCarlo and Cox, 2007). Our texture model incorporates an explicit form of invariance by representing all possible exemplars of a given texture (Figure S2) with a single set of statistic values. Moreover, different textures produce different statistics, providing an implicit form of selectivity. However, our model captures texture properties with a large number of simple statistics that are partially redundant. Humans, in contrast, categorize sounds into semantic classes, and seem to have conscious access to a fairly small set of perceptual dimensions. It should be possible to learn such lower-dimensional representations of categories from our sound statistics, combining the full set of statistics into a small number of “metastatistics” that relate to perceptual dimensions. We have found, for instance, that most of the variance in statistics over our collection of sounds can be captured with a moderate number of their principal components, indicating that dimensionality reduction is feasible.

The temporal averaging through which our texture statistics achieve invariance is appropriate for stationary sounds, and it is worth considering how this might be relaxed to represent sounds that are less homogeneous. A simple possibility involves replacing the global time-averages with averages taken over a succession of short time windows. The resulting local statistical measures would preserve some of the invariance of the global statistics, but would follow a trajectory over time, allowing representation of the temporal evolution of a signal. By computing measurements averaged within windows of many durations, the auditory system could derive representations with varying degrees of selectivity and invariance, enabling the recognition of sounds spanning a continuum from homogeneous textures to singular events.

## EXPERIMENTAL PROCEDURES

### Auditory Model

Our synthesis algorithm utilized a classic “subband” decomposition in which a bank of cochlear filters were applied to a sound signal, splitting it into frequency channels. To simplify implementation, we used zero-phase filters, with Fourier amplitude shaped as the positive portion of a cosine function. We used a bank of 30 such filters, with center frequencies equally spaced on an equivalent rectangular bandwidth (ERB)<sub>N</sub> scale (Glasberg and Moore, 1990), spanning 52–8844 Hz. Their (3 dB) bandwidths were comparable to those of the human ear (~5% larger than ERBs measured at 55 dB sound pressure level (SPL); we presented sounds at 70 dB SPL, at which human auditory filters are somewhat wider). The filters did not replicate all aspects of biological

auditory filters, but perfectly tiled the frequency spectrum—the summed squared frequency response of the filter bank was constant across frequency (to achieve this, the filter bank also included lowpass and highpass filters at the endpoints of the spectrum). The filter bank thus had the advantage of being invertible: each subband could be filtered again with the corresponding filter, and the results summed to reconstruct the original signal (as is standard in analysis-synthesis subband decompositions [Crochiere et al., 1976]).

The envelope of each subband was computed as the magnitude of its analytic signal, and the subband was divided by the envelope to yield the fine structure. The fine structure was ignored for the purposes of analysis (measuring statistics). Subband envelopes were raised to a power of 0.3 to simulate basilar membrane compression. For computational efficiency, statistics were measured and imposed on envelopes downsampled (following low-pass filtering) to a rate of 400 Hz. Although the envelopes of the high-frequency subbands contained modulations at frequencies above 200 Hz (because cochlear filters are broad at high frequencies), these were generally low in amplitude. In pilot experiments we found that using a higher envelope sampling rate did not produce noticeably better synthetic results, suggesting the high frequency modulations are not of great perceptual significance in this context.

The filters used to measure modulation power also had half-cosine frequency responses, with center frequencies equally spaced on a log scale (20 filters spanning 0.5–200 Hz), and a quality factor of 2 (for 3 dB bandwidths), consistent with those in previous models of human modulation filtering (Dau et al., 1997), and broadly consistent with animal neurophysiology data (Miller et al., 2002; Rodríguez et al., 2010). Although auditory neurons often exhibit a degree of tuning to spectral modulation as well (Depireux et al., 2001; Rodríguez et al., 2010; Schönwiesner and Zatorre, 2009), this is typically less pronounced than their temporal modulation tuning, particularly early in the auditory system (Miller et al., 2002), and we elected not to include it in our model. Because 200 Hz was the Nyquist frequency, the highest frequency filter consisted only of the lower half of the half-cosine frequency response.

We used a smaller set of modulation filters to compute the C1 and C2 correlations, in part because it was desirable to avoid large numbers of unnecessary statistics, and in part because the C2 correlations necessitated octave-spaced filters (see below). These filters also had frequency responses that were half-cosines on a log-scale, but were more broadly tuned ( $Q = \sqrt{2}$ ), with center frequencies in octave steps from 1.5625 to 100 Hz, yielding seven filters.

### Boundary Handling

All filtering was performed in the discrete frequency domain, and thus assumed circular boundary conditions. To avoid boundary artifacts, the statistics measured in original recordings were computed as weighted time-averages. The weighting window fell from one to zero (half cycle of a raised cosine) over the 1 s intervals at the beginning and end of the signal (typically a 7 s segment), minimizing artifactual interactions. For the synthesis process, statistics were imposed with a uniform window, so that they would influence the entire signal. As a result, continuity was imposed between the beginning and end of the signal. This was not obvious from listening to the signal once, but it enabled synthesized signals to be played in a continuous loop without discontinuities.

### Statistics

We denote the  $k^{\text{th}}$  cochlear subband envelope by  $s_k(t)$ , and the windowing function by  $w(t)$ , with the constraint that  $\sum_t w(t) = 1$ . The  $n^{\text{th}}$  modulation band of cochlear envelope  $s_k$  is denoted by  $b_{k,n}(t)$ , computed via convolution with filter  $f_n$ .

### Cochlear Marginal Statistics

Our texture representation includes the first four normalized moments of the envelope:

$$M1_k = \mu_k = \sum_t w(t) s_k(t),$$

$$M2_k = \frac{\sigma_k^2}{\mu_k^2} = \frac{\sum_t w(t) (s_k(t) - \mu_k)^2}{\mu_k^2},$$

$$M3_k = \frac{\sum_t w(t) (s_k(t) - \mu_k)^3}{\sigma_k^3},$$

and

$$M4_k = \frac{\sum_t w(t) (s_k(t) - \mu_k)^4}{\sigma_k^4} \quad k \in [1 \dots 32] \text{ in each case.}$$

The variance was normalized by the squared mean, so as to make it dimensionless like the skew and kurtosis.

The envelope variance, skew, and kurtosis reflect subband sparsity. Sparsity is often associated with the kurtosis of a subband (Field, 1987), and preliminary versions of our model were also based on this measurement (McDermott et al., 2009). However, the envelope's importance in hearing made its moments a more sensible choice, and we found them to capture similar sparsity behavior.

Figures 2D–2G show the marginal moments for each cochlear envelope of each sound in our ensemble. All four statistics vary considerably across natural sound textures. Their values for noise are also informative. The envelope means, which provide a coarse measure of the power spectrum, do not have exceptional values for noise, lying in the middle of the set of natural sounds. However, the remaining envelope moments for noise all lie near the lower bound of the values obtained for natural textures, indicating that natural sounds tend to be sparser than noise (see also Experiment 2b) (Attias and Schreiner, 1998).

### Cochlear Cross-Band Envelope Correlation

$$C_{jk} = \sum_t \frac{w(t) (s_j(t) - \mu_j) (s_k(t) - \mu_k)}{\sigma_j \sigma_k}, \quad j, k \in [1 \dots 32]$$

such that  $(k - j) \in [1, 2, 3, 5, 8, 11, 16, 21]$ .

Our model included the correlation of each cochlear subband envelope with a subset of eight of its neighbors, a number that was typically sufficient to reproduce the qualitative form of the full correlation matrix (interactions between overlapping subsets of filters allow the correlations to propagate across subbands). This was also perceptually sufficient: we found informally that imposing fewer correlations sometimes produced perceptually weaker synthetic examples, and that incorporating additional correlations did not noticeably improve the results.

Figure 3B shows the cochlear correlations for recordings of fire, applause, and a stream. The broadband events present in fire and applause, visible as vertical streaks in the spectrograms of Figure 4B, produce correlations between the envelopes of different cochlear subbands. Cross-band correlation, or “comodulation,” is common in natural sounds (Nelken et al., 1999), and we found it to be to be a major source of variation among sound textures. The stream, for instance, contains much weaker comodulation.

The mathematical form of the correlation does not uniquely specify the neural instantiation. It could be computed directly, by averaging a product as in the above equation. Alternatively, it could be computed with squared sums and differences, as are common in functional models of neural computation (Adelson and Bergen, 1985):

$$C_{jk} = \sum_t w(t) \frac{(s_j(t) - \mu_j + s_k(t) - \mu_k)^2 - (s_j(t) - \mu_j - s_k(t) + \mu_k)^2}{4\sigma_j \sigma_k}.$$

### Modulation Power

For the modulation bands, the variance (power) was the principal marginal moment of interest. Collectively, these variances indicate the frequencies present in an envelope. Analogous quantities appear to be represented by the modulation-tuned neurons common to the early auditory system (whose responses code the power in their modulation passband). To make the modulation power statistics independent of the cochlear statistics, we normalized each by the variance of the corresponding cochlear envelope; the measured statistics thus represent the proportion of total envelope power captured by each modulation band:

$$M_{k,n} = \frac{\sum_t w(t) b_{k,n}(t)^2}{\sigma_k^2}, \quad k \in [1 \dots 32], \quad n \in [1 \dots 20].$$

Note that the mean of the modulation bands is zero (because the filters  $f_n$  are zero-mean). The other moments of the modulation bands were either uninformative or redundant (see Supplemental Experimental Procedures) and were omitted from the model.

The modulation power implicitly captures envelope correlations across time, and is thus complementary to the cross-band correlations. Figure 3A shows the modulation power statistics for recordings of swamp insects, lake shore waves, and a stream.

### Modulation Correlations

These correlations were computed using octave-spaced modulation filters (necessitated by the C2 correlations), the resulting bands of which are denoted by  $\tilde{b}_{k,n}(t)$ .

The C1 correlation is computed between bands centered on the same modulation frequency but different acoustic frequencies:

$$C1_{j,k,n} = \frac{\sum_t w(t) \tilde{b}_{j,n}(t) \tilde{b}_{k,n}(t)}{\sigma_{j,n} \sigma_{k,n}}, \quad j \in [1 \dots 32], \quad (k - j) \in [1, 2], \quad n \in [2 \dots 7],$$

and

$$\sigma_{j,n} = \sqrt{\sum_t w(t) \tilde{b}_{j,n}(t)^2}.$$

We imposed correlations between each modulation filter and its two nearest neighbors along the cochlear axis, for six modulation bands spanning 3–100 Hz.

C1 correlations are shown in Figure 3C for the sounds of waves and fire. The qualitative pattern of C1 correlations shown for waves is typical of a number of sounds in our set (e.g., wind). These sounds exhibit low-frequency modulations that are highly correlated across cochlear channels, but high-frequency modulations that are largely independent. This effect is not simply due to the absence of high-frequency modulation, as most such sounds had substantial power at high modulation frequencies (comparable to that in pink noise, evident from dB values close to zero in Figure 3A). In contrast, for fire (and many other sounds), both high and low frequency modulations exhibit correlations across cochlear channels. Imposing the C1 correlations was essential to synthesizing realistic waves and wind, among other sounds. Without them, the cochlear correlations affected both high and low modulation frequencies equally, resulting in artificial sounding results for these sounds.

C1 correlations did not subsume cochlear correlations. Even when larger numbers of C1 correlations were imposed (i.e., across more offsets), we found informally that the cochlear correlations were necessary for high quality synthesis.

The second type of correlation, labeled C2, is computed between bands of different modulation frequencies derived from the same acoustic frequency channel. This correlation represents phase relations between modulation frequencies, important for representing abrupt onsets and other temporal asymmetries. Temporal asymmetry is common in natural sounds, but is not captured by conventional measures of temporal structure (e.g., the modulation spectrum), as they are invariant to time reversal (Irino and Patterson, 1996). Intuitively, an abrupt increase in amplitude (e.g., a step edge) is generated by a sum of sinusoidal envelope components (at different modulation frequencies) that are aligned at the beginning of their cycles (phase  $-\pi/2$ ), whereas an abrupt decrease is generated by sinusoids that align at the cycle midpoint (phase  $\pi/2$ ), and an impulse (e.g., a click) has frequency components that align at their peaks (phase 0). For sounds dominated by one of these feature types, adjacent modulation bands thus have consistent relative phase in places where their amplitudes are high. We captured this relationship with a complex-valued correlation measure (Portilla and Simoncelli, 2000).

We first define analytic extensions of the modulation bands:

$$\alpha_{k,n}(t) \equiv \tilde{b}_{k,n}(t) + iH\left(\tilde{b}_{k,n}(t)\right),$$

where  $H$  denotes the Hilbert transform and  $i = \sqrt{-1}$ .

The analytic signal comprises the responses of the filter and its quadrature twin, and is thus readily instantiated biologically. The correlation has the standard form, except it is computed between analytic modulation bands tuned to modulation frequencies an octave apart, with the frequency of the

lower band doubled. Frequency doubling is achieved by squaring the complex-valued analytic signal:

$$d_{k,n}(t) = \frac{a_{k,n}^2(t)}{\|a_{k,n}(t)\|},$$

yielding

$$C2_{k,mn} = \frac{\sum_t w(t) d_{k,m}^*(t) a_{k,n}(t)}{\sigma_{k,m} \sigma_{k,n}},$$

$k \in [1 \dots 32]$ ,  $m \in [1 \dots 6]$ , and  $(n - m) = 1$ , where  $*$  and  $\|\cdot\|$  denote the complex conjugate and modulus, respectively.

Because the bands result from octave-spaced filters, the frequency doubling of the lower-frequency band causes them to oscillate at the same rate, producing a fixed phase difference between adjacent bands in regions of large amplitude. We use a factor of 2 rather than something smaller because the operation of exponentiating a complex number is uniquely defined only for integer powers. See Figure S6 for further explanation.

$C2_{k,mn}$  is complex valued, and the real and imaginary parts must be independently measured and imposed. Example sounds with onsets, offsets, and impulses are shown in Figure 3D along with their C2 correlations.

In total, there are 128 cochlear marginal statistics, 189 cochlear cross-correlations, 640 modulation band variances, 366 C1 correlations, and 192 C2 correlations, for a total of 1515 statistics.

### Imposition Algorithm

Synthesis was driven by a set of statistics measured for a sound signal of interest using the auditory model described above. The synthetic signal was initialized with a sample of Gaussian white noise, and was modified with an iterative process until it shared the measured statistics. Each cycle of the iterative process, as illustrated in Figure 4A, consisted of the following steps:

- (1) The synthetic sound signal is decomposed into cochlear subbands.
- (2) Subband envelopes are computed using the Hilbert transform.
- (3) Envelopes are divided out of the subbands to yield the subband fine structure.
- (4) Envelopes are downsampled to reduce computation.
- (5) Envelope statistics are measured and compared to those of the original recording to generate an error signal.
- (6) Downsampled envelopes are modified using a variant of gradient descent, causing their statistics to move closer to those measured in the original recording.
- (7) Modified envelopes are upsampled and recombined with the unmodified fine structure to yield new subbands.
- (8) New subbands are combined to yield a new signal.

We performed conjugate gradient descent using Carl Rasmussen's "minimize" MATLAB function (available online). The objective function was the total squared error between the synthetic signal's statistics and those of the original signal. The subband envelopes were modified one-by-one, beginning with the subband with largest power, and working outwards from that. Correlations between pairs of subband envelopes were imposed when the second subband envelope contributing to the correlation was being adjusted.

Each episode of gradient descent resulted in modified subband envelopes that approached the target statistics. However, there was no constraint forcing the envelope adjustment to remain consistent with the subband fine structure (Ghitza, 2001), or to produce new subbands that were mutually consistent (in the sense that combining them would produce a signal that would yield the same subbands when decomposed again). It was thus generally the case that during the first few iterations, the envelopes measured at the beginning of cycle  $n + 1$  did not completely retain the adjustment imposed at cycle  $n$ , because combining envelope and fine structure, and summing up the subbands, tended to change the envelopes in ways that altered their statistics. However, we found that with iteration, the envelopes generally converged to a state with the desired statistics. The fine structure was not directly constrained, and relaxed to a state consistent with the envelope constraints.

Convergence was monitored by computing the error in each statistic at the start of each iteration and measuring the signal-to-noise ratio (SNR) as the ratio

of the squared error of a statistic class, summed across all statistics in the class, to the sum of the squared statistic values of that class. The procedure was halted once all classes of statistics were imposed with an SNR of 30 dB or higher or when 60 iterations were reached. The procedure was considered to have converged if the average SNR of all statistic classes was 20 dB or higher. Occasionally the synthesis process converged to a local minimum in which it failed to produce a signal matching the statistics of an original sound according to our criterion. This was relatively rare, and such failures of convergence were not used in experiments.

Although the statistics in our model constrain the distribution of the sound signal, we have no explicit probabilistic formulation and as such are not guaranteed to be drawing samples from an explicit distribution. Instead, we qualitatively mimic the effect of sampling by initializing the synthesis with different samples of noise (as in some visual texture synthesis methods) (Heeger and Bergen, 1995; Portilla and Simoncelli, 2000). An explicit probabilistic model could be developed via maximum entropy formulations (Zhu et al., 1997), but sampling from such a distribution is generally computationally prohibitive.

### SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, six figures, and one table and can be found with this article online at doi:10.1016/j.neuron.2011.06.032.

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